

Lower Cretaceous brachiopods from Provence, France, and their biostratigraphical distribution

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Synopsis

Articulate brachiopods from the Berriasian and Valanginian succession south of Castellane, Provence are described, including four new species: a rhynchonellid *Rhynchonella cotilloni*, a terebratuloid *Sellithyris? middlemissi*, and two dallinoids *Rugitela? rotunda* and *Advenina oweni* (type species of the new genus *Advenina*). These new species are stratigraphically distinct, and *Rhynchonella* s.s. is shown to have a representative outside of the Boreal Realm. Brachiopod speciation appears to be associated with the Lower Cretaceous marine transgressions in Provence.

Introduction

In the Lower Cretaceous sediments of the Arc of Castellane brachiopods are locally abundant. Pajaud (1974) has described brachiopods from this region which Cotillon (1971) had already found useful within a regional biostratigraphy for the Arc of Castellane. By taking transverse serial sections of duplicate material it has been possible to determine the generic affinities of some of these species. The brachiopods described here were collected from Carajuan, Point Sublime and Collet des Boules, Alpes de Haute-Provence (Figs 1–2), and also from the departments of Var and Isère, and a few specimens from near Ste Croix, Switzerland.

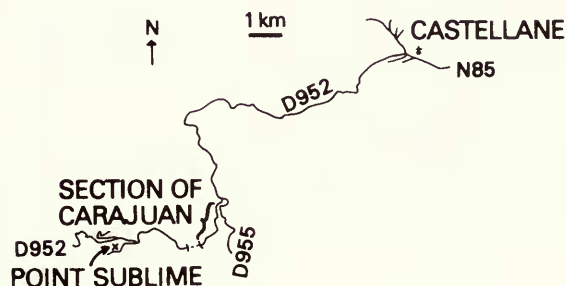
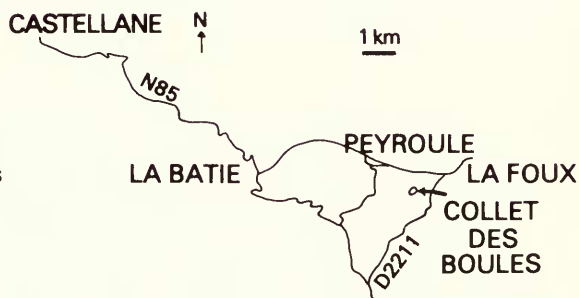


Fig. 1 Locality map for the section at Carajuan and Point Sublime, Alpes de Haute-Provence.

Fig. 2 Locality map for Collet des Boules, Alpes de Haute-Provence.



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The brachiopods are deposited in the British Museum (Natural History) unless otherwise stated (prefix BB). Material has also been available for study from the collections of Lyon, Neuchâtel and Grenoble Universities, Dr F. A. Middlemiss of Queen Mary College London, and from my own collection (prefix MS). All specimen dimensions are given in mm; L = length, W = width, T = thickness.

In the synonymies annotations follow the convention of Matthews (1973).

Stratigraphy

The succession at Carajuan, where much of the material described in this paper was collected, provides an excellent section through the Provençal facies of the Lower Cretaceous in the Arc of Castellane. This is shown in Fig. 3, based on an unpublished figure prepared for a study leaflet issued by the Pre-Albian Stages Working Group in 1979. At Carajuan the thickness of the succession from the Tithonian to the top of the Barremian is approximately 350 metres. Bed 10 of Barremian age, beds 9 and 8 ('Grande Lumachelle', L2 of Fig. 3) of Hauterivian age and bed 7 of Upper Valanginian age have not formed part of the present study. The ammonite *Saynoceras verrucosum* is found in the basal horizon of bed 7.

Bed 6, 'Petite Lumachelle' (L1 of Fig. 3) forms a hard cap to the underlying shales, and a hard-ground is developed in this yellow limestone. From this bed fifteen specimens of *Musculina sanctaerucis* (Catzigras) were collected. The uniplicate anterior commissure, which is not typical of the species, of three of these necessitated investigation of their internal structures. Bed 6 is rich in fossils, including echinoids (*Toxaster* sp.), bivalves (including *Trigonia* sp. and *Exogyra* sp.) and gastropods.

Bed 5 comprises grey shales which yield a patchily abundant terebratulid referred to herein as *Advenina oweni* gen. et sp. nov. (p. 188). It is externally homoeomorphic with other Lower Cretaceous terebratulids but is shown to be generically distinct from them by its internal structures. At Carajuan *A. oweni* is associated with a clay-rich lithofacies and other brachiopods are uncommon. *Exogyra couloni* DeFrance is recorded from this bed and may have offered a suitable substrate for the brachiopods, although the small size of *A. oweni* would assist its stability on a soft substrate. The terebratulids *Loriolithyris valdensis* (de Loriol) and *Cruralina? biauriculata* (d'Orbigny) are uncommon in bed 5. The echinoid *Toxaster retusus* (Lamarck) is commonly found in this bed. Beds 5 and 6 are of late Lower Valanginian age, from the ammonite evidence of beds 7 and 4. The ammonite *Saynoceras verrucosum* from bed 7 occurs 'at the very base of the late Valanginian, always in an argillaceous lithofacies probably corresponding with an important transgression' (Kemper, Rawson & Thieuloy 1981: 277).

Bed 4 consists of yellow shales and shaly limestones. The ammonite *Karakaschiceras* sp. is present in a half-metre band (K of Fig. 3), indicating a late Lower Valanginian age at Carajuan: Kemper, Rawson & Thieuloy (1981: 282) gave the age of *Karakaschiceras* as late early Valanginian to early late Valanginian.

Bed 3, alternating shales and shaly limestones with some nodular horizons, has yielded the ammonite *Thurmanniceras campylotoxus* (Uhlig), which indicates a Lower Valanginian age.

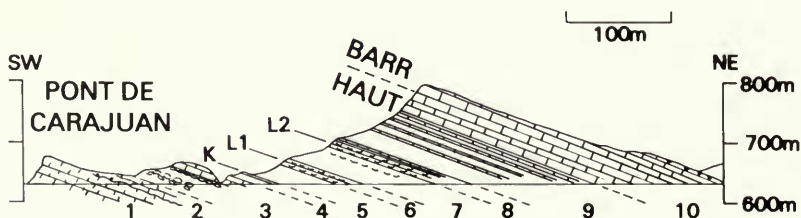


Fig. 3 The section at Carajuan, Alpes de Haute-Provence. The base line represents the course of the road D952. K = *Karakaschiceras* sp., L1 = Petite Lumachelle, L2 = Grande Lumachelle. Beds numbered 1 to 10.

Bed 2 comprises blue-grey micritic flaggy limestone, representing the start of marine sedimentation in the Lower Cretaceous. The new species *Rhynchonella cotilloni*, *Rugitela? rotunda* and *Sellithyris? middlemissi* are found in this bed, of which *R. cotilloni* was the most abundant macrofaunal element collected at Carajuan and Point Sublime. The brachiopod species from this horizon are all small, rarely greater than 1 cm in length, width or thickness. *R. cotilloni* may have been the most successful brachiopod in this environment. *Rugitela? rotunda* is a rare element in this fauna, only known from three specimens at Point Sublime, but present in a similar lithofacies north of Trigance, Var. Another diminutive species is represented by rare specimens of *Sellithyris? middlemissi*. The small size of these brachiopods may reflect winnowing from a nearby region, but the shells are well preserved and transport would have been over only a short distance. The small size of *Rhynchonella cotilloni* and *Rugitela? rotunda* is not confined to the sediments of Point Sublime, it is noted from other localities in Provence. This brachiopod fauna may provide an example of Cope's Rule (Cooper 1977) whereby transgressions are characterized by small forms. The ammonite *Berriasella?* gives an indication of a Berriasian age for bed 2 (M. K. Howarth, personal communication). Fragments of echinoid radiole and a belemnite (aff. *Duvalia conica* Blainville) are the only other macrofaunal elements which have been observed in my study of bed 2 at Carajuan.

At Carajuan the Tithonian white limestones (bed 1 of Fig. 3), containing nerineids, corals, echinoid radioles, bryozoa and stromatolites, are overlain by Lower Cretaceous sediments which show evidence of non-sequence at their base. In the 'calcaire blancs' facies of the uppermost Jurassic and lowermost Cretaceous of this region Cotillon (1971: 38) says it is practically impossible to delimit the Portlandian and Berriasian. The start of the Cretaceous was taken by Cotillon as thickly bedded limestones with intercalated green clays, which are found above 20–40 m of compact beds with the terebratulid *Weberithyris moravica* (Glocker) (= Tithonian).

Cotillon (1975) records the Berriasian gastropod *Ampullina leviathan* (Pictet & Campiche) from the micritic limestones of Provence (bed 2, Fig. 3). The Middle Parves Beds of the southern French Jura (Ager & Evamy 1963) also contain this Berriasian gastropod and may be the lateral equivalents of bed 2 (Fig. 3) in Provence. In the southern French Jura I have collected from the Berriasian Middle Parves Beds at Gélignieux near Belley, Ain, the brachiopods *Sellithyris carteroniana* (d'Orbigny) and *Loriolithyris valdensis* (de Loriol). These two terebratulid species confirm the Lower Cretaceous age of the Middle Parves Beds, which are in part ferruginous oolitic bioclastic limestones up to 20 m thick. This laterally discontinuous horizon may be a thicker development of the basal Cretaceous 'Unité inférieure oolithique' of Berriasian age in the Swiss Jura (Steinhauser & Charollais 1971). The latter unit includes Baumberger & Moulin's (1899) bed 5, from which they recorded two commonly occurring brachiopods, '*Terebratula*' *valdensis* and '*T.*' cf. *carteroniana*. These do not provide conclusive evidence of the Lower Cretaceous stage to which these oolitic sediments of the central Swiss and southern Jura belong as they are long-ranging species, but they do give an indication of a similar environmental setting in these areas.

The base of the Jacobi/Grandis ammonite Zone has been taken as the base of the Cretaceous and Berriasian herein (Flandrin 1975: 392).

Systematic descriptions

Order **RHYNCHONELLIDA** Kuhn, 1949

Superfamily **RHYNCHONELLACEA** Gray, 1848

Family **RHYNCHONELLIDAE** Gray, 1848

Subfamily **RHYNCHONELLINAE** Gray, 1848

EMENDED DIAGNOSIS (adapted from Ager, 1965). Shell cynocephalous to uniplicate, with strong dorsal fold. Smooth stage posteriorly, with few to many costae anteriorly, crura radulifer.

RANGE OF SUBFAMILY. Triassic to Lower Cretaceous.

Genus *RHYNCHONELLA* Fischer, 1809

TYPE SPECIES. *Rhynchonella loxiae* Fischer 1809.

EMENDED DIAGNOSIS (adapted from Ager, 1965). Small to medium in size, triangular; dorsal fold high to gently uniplicate. Costae few to numerous, usually with smooth neanic stage posteriorly. Beak small. Dental lamellae well developed, septalium shallow. Dorsal septum short or absent. Crura radulifer. Shell mosaic may be seen on internal casts.

RANGE OF GENUS. Oxfordian to Barremian.

REMARKS. In a revision of the genus *Rhynchonella* s.s. Ager (1957) gave serial sections of *R. loxiae*, the type species. *R. proeminens* Yin (1931: 154; pl. XVIII, figs 12, 12a-c) was erected by Yin for one specimen from the Tithonian of Col de Ferrières, southern France. Yin's figures indicate that it has subangular costae, twelve on the brachial valve and ten (?) on the pedicle valve. There is a well-developed brachial fold with three costae on it. The pedicle umbo is suberect and there appears to be a small posteriorly smooth area on both valves. From its external characters this species appears to belong to *Rhynchonella* s.s.

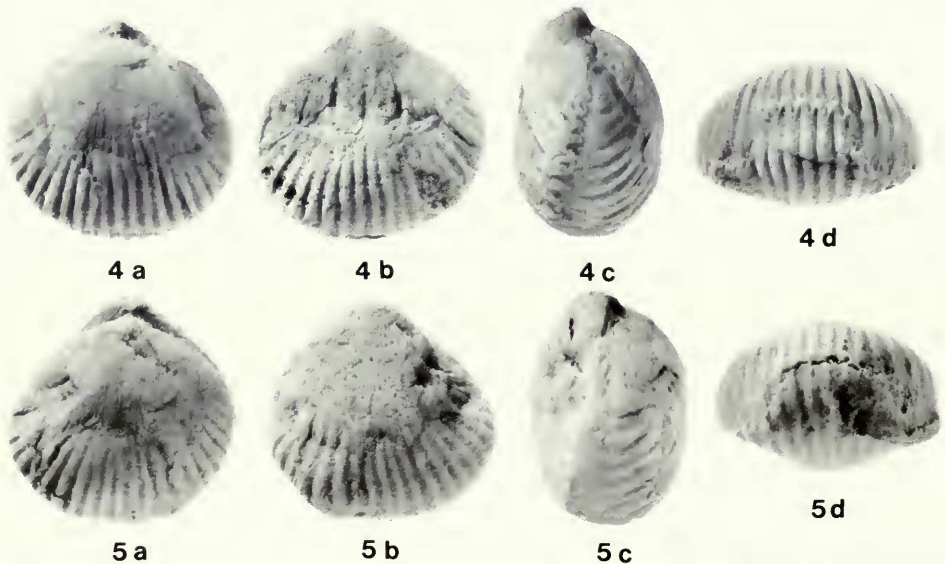
Rhynchonella cotilloni sp. nov.

Figs 4-7

- v? 1913 *Rhynchonella corallina* Leymerie sp. var. *neocomiensis* Jacob & Fallot: 50; pl. VI, figs 9-11; non figs 12-15.
 non 1931 *Rhynchonella corallina* var. *neocomiensis* Jacob & Fallot; Yin: 153; pl. XVIII, figs 5-6.
 1971 '*Rhynchonella*' cf. *corallina* var. *neocomiensis* Jacob & Fallot; Cotillon: 301.
 1974 '*Rhynchonella*' *neocomiensis* Jacob & Fallot cf. *corallina* Leymerie; Pajaud: 96, fig. Y; pl. 1, fig. Y.

HOLOTYPE. BB82400 from the Berriasian of Point Sublime, Alpes de Haute-Provence, France. Dimensions (mm): L 10.6, W 10.9, T 7.0.

PARATYPES. BB82401-6 from the Berriasian of Carajuan, France; from bed 2 of Fig. 3. BB82407-8 from the same horizon and locality as the holotype. MS/L 1588 from the Upper Valanginian north of Trigance, Var; Lyon University Collection. Dimensions (mm): BB82401



Figs 4-5 *Rhynchonella cotilloni* sp. nov., Berriasian. Fig. 4a-d, holotype, BB82400; Point Sublime, Alpes de Haute-Provence. $\times 3$. Fig. 5a-d, paratype, BB82403; Carajuan, Alpes de Haute-Provence. $\times 3$.

L 10.5, W 10.6, T 6.8; BB82402 (sectioned; Fig. 7) L 10.4, W 10.4, T 6.6; BB82403 L 10.6, W 10.7, T 7.2; BB82404 L 10.4, W 11.6, T 7.8; BB82405 L 10.2, W 10.2, T 7.6; BB82406 L 9.5, W 9.8, T 6.7; BB82407 L 11.1, W 12.1, T 7.9; BB82408 damaged; MS/L 1588 L 11.0, W 11.4, T 7.3.

NAME. After Pierre Cotillon who has worked on the Lower Cretaceous of the Arc of Castellane.

DIAGNOSIS. *Rhynchonella* of subtriangular to subcircular outline. Width usually equal to or slightly greater than length. Maximum width just anterior of mid-length. Biconvex profile, pedicle valve flatter. Fine ribbing on both valves with smooth umbonal areas posteriorly. Uniplicate anterior commissure. Internal structures as for genus.

DESCRIPTION. The relationships between length, width and thickness are shown in Fig. 6. The brachial valve has its greatest convexity in the posterior third and anterior quarter of lateral profile. The pedicle umbo is suberect and the pedicle foramen small, circular and hypothryid, with two small triangular deltidial plates. Beak ridges are well defined and delimit a quite wide concave interarea. The brachial valve has between 19 and 26 ribs with four to eight on the fold. The pedicle valve has between 18 and 25 ribs, with three to six in the sulcus.

The smooth area of the neanic stage covers about one-third to half of the length of both valves. This smooth area has no discernible ribs, but is covered by fine 'striae'. These are the calcite fibres of the shell, lying at an oblique angle to the shell surface, as noted by Ager (1957: 6) in *Rhynchonella loxiae* Fischer and *R. rouillieri* Eichwald, and are particularly noticeable where shell has flaked away.

Internal characters. One series of transverse serial sections is presented here (Fig. 7). The hinge plates developed horizontally and diverged anteriorly. They are only weakly deflected from the inner socket ridges (Fig. 7, section 1.6 mm). Crural base attachment is on the inner edge of the hinge plates, dorsally directed. The crura extend anteriorly as dorsomedially concave, right-angled projections and are of radulifer type (Ager 1957, 1965, 1971, Owen & Thurrell 1968).

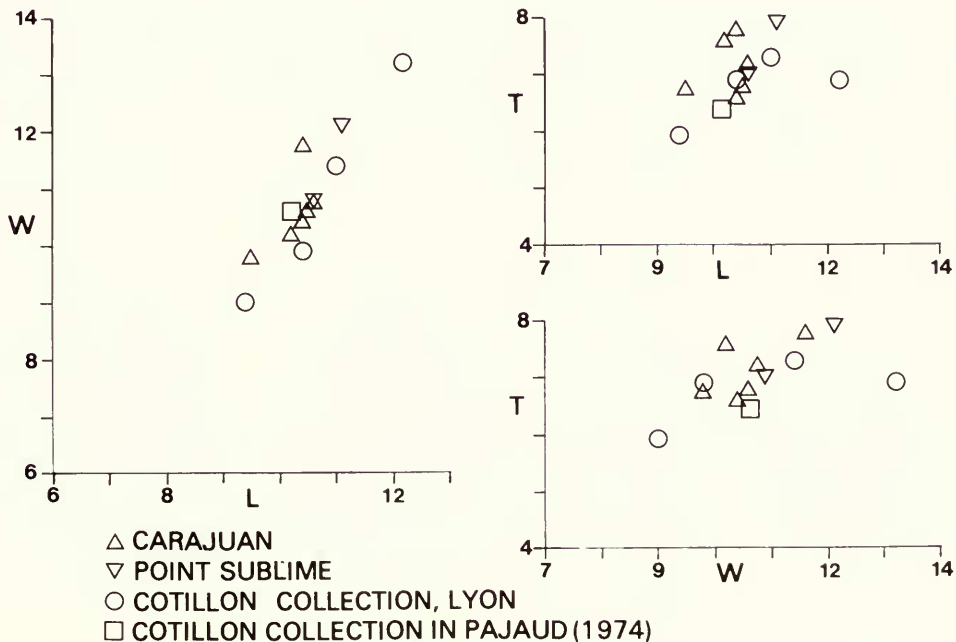


Fig. 6 Plots of Length against Width, Length against Thickness, and Width against Thickness for *Rhynchonella cotilloni* sp. nov. Dimensions in mm.

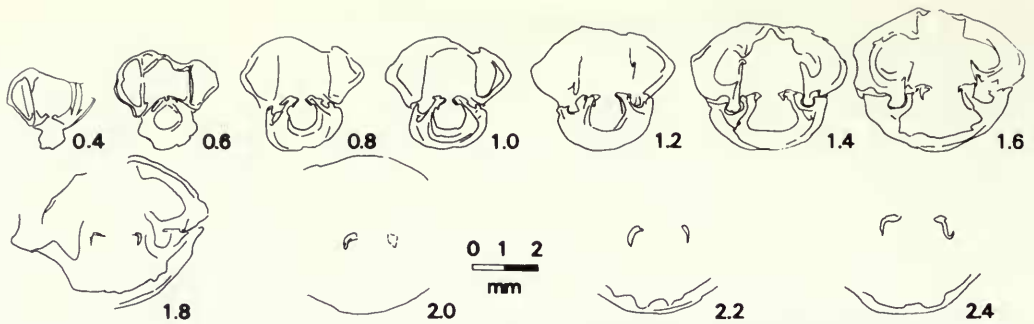


Fig. 7 Transverse serial sections through a paratype (BB82402) of *Rhynchonella cotilloni* sp. nov., Berriasian of Carajuan, Alpes de Haute-Provence. Dimensions (mm): L 10.4, W 10.4, T 6.6.

REMARKS. Jacob & Fallot (1913) gave two localities for *R. corallina* Leymerie sp. var. *neocomiensis*: Echaillon-les-Bains, Isère, and Mont Salève, Haute Savoie, France. The dimensions (mm) of three specimens from the Valanginian of Echaillon-les-Bains were given by Jacob & Fallot (1913: 50) as: L 19.0, W 19.5, T 13.0; L 20.0, W 23.8, T 12.0; L 24.0, W 24.0, T 14.0. These specimens are larger than *R. cotilloni* sp. nov.; they are also more coarsely ribbed and develop an asymmetrical anterior commissure. These specimens, figured by Jacob & Fallot (1913: pl. VI, figs 12–15) are taken as the syntypes of their var. *neocomiensis*. On the same plate (1913: pl. VI, figs 9–11) they figured material from the Berriasian of Mont Salève, immediately above the 'Purbeckian', and these are comparable in size to *R. cotilloni*. However, the latter species has finer ribbing, a large smooth area posteriorly on both valves, and a less protruding pedicle umbo.

Other rhynchonellids figured by Jacob & Fallot (1913) from the Cretaceous of south-east France closely resemble *R. cotilloni* sp. nov. *Burrirhynchia? gibbsiana* (Sow.) var. *sayni* Jacob & Fallot (1913: 63; pl. XI, figs 1–6, especially fig. 5) from the Barremian of Saynes, Gard, is very similar to *R. cotilloni* but has more ribs and appears to lack the smooth umbonal area present on the latter species. The juvenile specimen of '*R.*' *lata* d'Orbigny var. *minor* Jacob & Fallot (1913: 57; pl. VIII, fig. 18) from the Couche à Orbitolines du Fâ, near St Pierre-de-Chérennes, Isère, is externally similar to *R. cotilloni* in dimensions, ribbing, and its anterior fold. Burri (1956) referred this variety to *Lamellaerhynchia picteti* Burri; it has a more elongate pedicle umbo than *R. cotilloni* and has an exposed circular foramen.

R. parkhillensis Owen & Thurrell (1968) has fewer ribs than *R. cotilloni* but shares a smooth neanic stage. This latter feature has rightly been given much taxonomic significance (Ager 1965: H610 and 1971: 397).

Pajaud wrote (1974: 97) that the binomen '*Rhynchonella*' *neocomiensis* Jacob & Fallot was used for convenience for the forms from the Valanginian of Bargême, Alpes de Haute-Provence. His pl. 1, fig. Y gives a brachial view only of a specimen of the species described here as *R. cotilloni*, in which the ribbing is too fine for Jacob & Fallot's var. *neocomiensis*.

The median septum is variously developed in *Rhynchonella* s.s. and its development is incipient or lacking in *R. cotilloni*.

HORIZON AND LOCALITIES. The specimens from Carajuan were collected from bed 2 (Fig. 3), and from the same horizon at Point Sublime. Cotillon (1971) and Pajaud (1974) make no reference to the terebratulids and terebratellids associated with *R. cotilloni*, namely *Sellithyris? middlemissi* sp. nov. (opposite) and *Rugitela? rotunda* sp. nov. (p. 186). A fragment of a belemnite guard (aff. *Duvalia conica* Blainville; determined P. Doyle) was also collected at Carajuan.

Preservation of the rhynchonellids varies from complete and uncrushed to crushed and distorted; the majority of specimens appear distorted by diagenetic effects. Only a single pedicle valve has been found disarticulated.

Rhynchonella cotilloni sp. nov. is known only from the Berriasian of Provence and the Upper Valanginian of Var.

MATERIAL. From the Berriasian of Point Sublime (bed 2 of Fig. 3) four specimens, BB82400 (holotype), BB82407–8, MS 1017. Twenty specimens from the same horizon at Carajuan, MS 0165–78, including six paratypes, BB82401–6. Five specimens from the Upper Valanginian, north of Trigance, Var (Lyon University Collection), including one paratype, MS/L 1588.

Order **TEREBRATULIDA** Waagen, 1883

Suborder **TEREBRATULIDINA** Waagen, 1883

Superfamily **TEREBRATULACEA** Gray, 1840

Family **TEREBRATULIDAE** Gray, 1840

Subfamily **SELLITHYRIDINAE** Muir-Wood, 1965

Genus **SELLITHYRIS** Middlemiss, 1959

TYPE SPECIES. *Terebratula sella* J. de C. Sowerby 1823.

Sellithyris? *middlemissi* sp. nov.

Figs 8, 9

HOLOTYPE. BB82398, from the Berriasian of Point Sublime, Alpes de Haute-Provence. Dimensions (mm): L 14.5, W 11.9, T 7.7.

PARATYPE. BB82399 (sectioned; Fig. 9) from the same horizon and locality as the holotype. Dimensions (mm): L 12.4, W 10.0, T 6.5.

NAME. For Dr F. A. Middlemiss, who also donated the specimens.

DIAGNOSIS. *Sellithyris?* of sub-pentagonal to elongate-oval outline. Biconvex profile. Suberect pedicle umbo with short, subrounded beak ridges. Small circular mesothyrid pedicle foramen, symphytium(?) poorly developed. Lateral commissure dorsally arched, anterior commissure broadly uniplicate. Adductor muscle scars on brachial valve long, thin and parallel. Internal structures as for the genus (Middlemiss 1976: 39).

DESCRIPTION. The internal structures of one specimen have been investigated by serial sectioning (Fig. 9). The cardinal process is large, considering the small size of the specimen. The hinge plates are cuneate and ventrally concave, with small crural bases. There is a slight angular deflection of the hinge plate and inner socket ridge. The crural processes are sub-parallel.

REMARKS. The small size, lack of biplication, and relatively large adductor muscle scars suggest that these specimens are juveniles. However, the massive cardinal process is a feature usually associated with maturing or adult terebratulids.

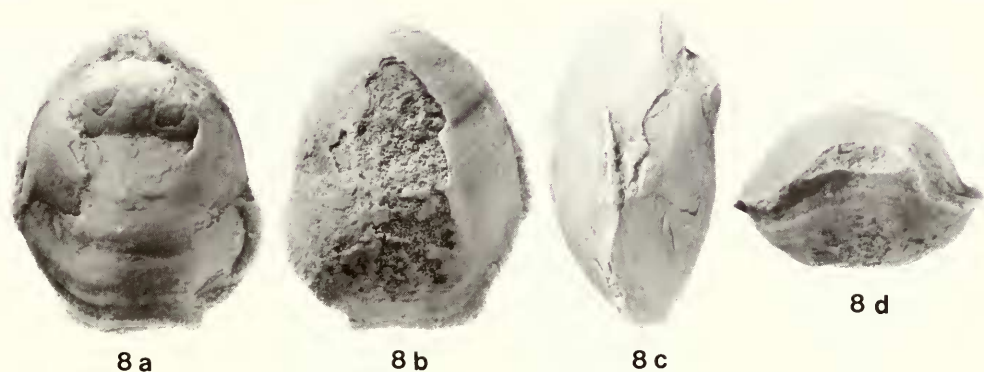


Fig. 8a–d *Sellithyris?* *middlemissi* sp. nov., Berriasian. **Holotype**, BB82398; Point Sublime, Alpes de Haute-Provence. $\times 3$.

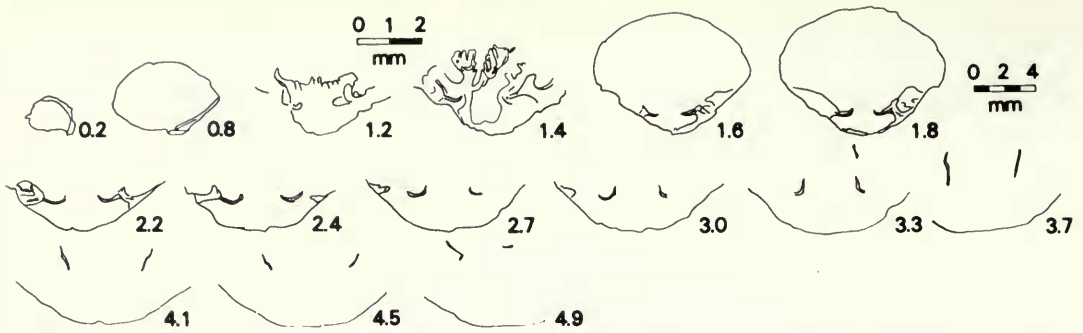


Fig. 9 Transverse serial sections through a paratype (BB82399) of *Sellithyris? middlemissi* sp. nov., Berriasian of Point Sublime, Alpes de Haute-Provence. Sections 1.2 mm and 1.4 mm are shown enlarged. Dimensions (mm): L 12.4, W 10.0, T 6.5.

The species appears distinct from others in the Sellithyridinae. The rounded posterior outline distinguishes it from *Loriolithyris valdensis* (de Loriol). Internally *S.? middlemissi* possesses a strongly developed cardinal process. It lacks the piped hinge plates as well as the initial marked deflection of the hinge plates and inner socket ridges of *Loriolithyris*. Investigation of more material of *S.? middlemissi* may allow a better understanding of the variability in this species.

HORIZON. Berriasian of Provence. The two specimens only.

Genus *MUSCULINA* Schuchert & Le Vene, 1929

TYPE SPECIES. *Terebratula biplicata acuta* von Buch [= *Musculina sanctaerucis* (Catzigras, 1948)] (non *Terebratula acuta* Sowerby, 1816). Dieni, Middlemiss & Owen (1975: 181) discussed the naming of the type species.

Musculina sanctaerucis (Catzigras)

Figs 10, 11

- 1834 *Terebratula biplicata acuta* von Buch: 108.
- 1851 *Terebratula biplicata acuta* von Buch; Quenstedt: 473; pl. 38, fig. 2 (as *T. acuta*).
- v 1872 *Terebratula acuta* Quenstedt; Pictet & de Loriol: 14; pl. 202, figs 14–18.
- * 1948 *Terebratula sanctae crucis* Catzigras: 391; fig. 1 (1–4, 8, 10, 12, 15–17, 19).
- v 1965 *Musculina biennensis* Muir-Wood: H793; figs 658 (1), 659 (2).
- v 1968 *Musculina sanctaerucis* (Catzigras) Middlemiss: 19; fig. 9, pl. B, figs 3–4.
- v 1975 *Musculina sanctaerucis* (Catzigras); Dieni, Middlemiss & Owen: 179; pl. 32, figs 12–15.
- v 1976 *Musculina sanctaerucis* (Catzigras); Middlemiss: 53; pl. 5, figs 7–8, pl. 6, figs 1–3.

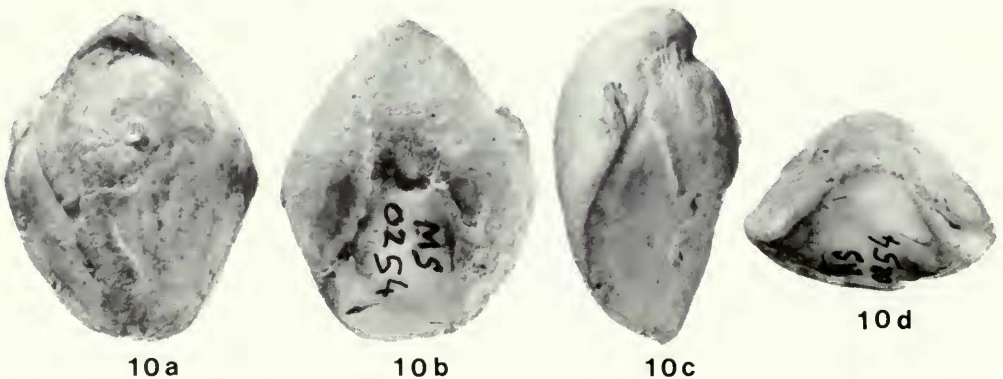


Fig. 10a–d *Musculina sanctaerucis* (Catzigras), Lower Valanginian. Plaster cast of sectioned specimen BB86867; Carajuan, Alpes de Haute-Provence. $\times 3$.

HOLOTYPE. The specimen figured by Quenstedt (1851: pl. 38, fig. 2) from the Neocomian of Neuchâtel, Switzerland, and preserved in the Geological-Palaeontological Institute and Museum, Tübingen (No. 48.70).

DIAGNOSIS. In the emended diagnosis of Middlemiss (1976: 52) only the following needs to be changed: 'Anterior commissure sulciplicate' emended to 'Anterior commissure rarely uniplicate to sulciplicate'.

DESCRIPTION. The species was described in detail by Middlemiss (1976). Material from the Lower Valanginian of Provence, the species' earliest known occurrence (Middlemiss 1981: 716), has been studied. From the Petite Lumachelle, Carajuan (bed 6 of Fig. 3) specimens of *M. sanctaerucis* were collected, appearing slightly wider and thicker than specimens from the Marne d'Hauterive of the French and Swiss Jura. The pedicle umbo is more erect and the symphytium not so large in the present Provençal specimens. These distinctions may reflect stratigraphical or ecological differences.

Three specimens from Carajuan have a uniplicate anterior commissure, as opposed to the sulciplicate form typically seen in *M. sanctaerucis*. Externally they are very similar to the sulciplicate specimens and grade into weakly biplicate forms. One of them has been serially sectioned (Fig. 11) and shows that the uniplicate specimens are variants within the limits of specific variation of the species *Musculina sanctaerucis*. I see little point in proposing a sub-species based on three specimens that thus blend into typically sulciplicate forms.

Silicification has affected the results obtained from sectioning but the strongly concave hinge plates, clubbed crural bases, sub-parallel crural processes and the arched transverse band are typical of the genus.

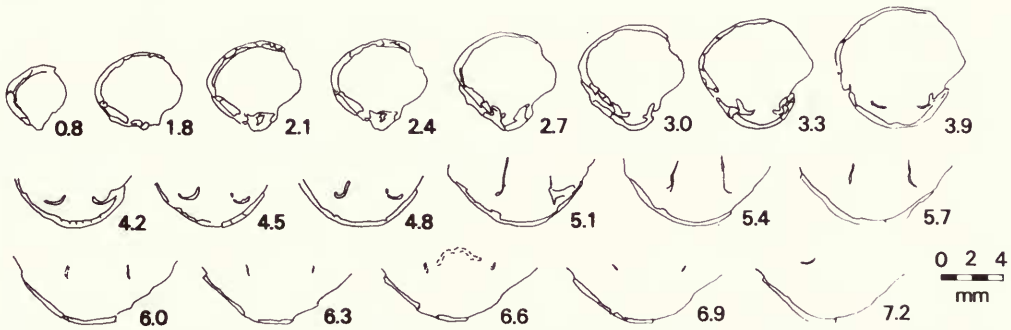


Fig. 11 Transverse serial sections through a specimen (BB86867) of *Musculina sanctaerucis* (Catzigras); Lower Valanginian of Carajuan, Alpes de Haute-Provence. Dimensions (mm): L 15.3, W 12.2, T 8.3.

HORIZON AND LOCALITY. Bed 6 (Fig. 3), the Petite Lumachelle, Carajuan; Lower Valanginian. Middlemiss (1981: 716) gave a detailed account of this species' distribution.

MATERIAL. Fifteen complete specimens (MS 0253, MS 0255–67, BB86867 (sectioned; Fig. 11)), three with a uniplicate anterior commissure (BB86867, MS 0255–6). Nineteen fragmentary specimens (MS 0268–87).

Suborder **TEREBRATELLIDINA** Muir-Wood, 1955

Superfamily **DALLINOIDEA** Beecher, 1893

Family **DALLINIDAE** Beecher, 1893

Subfamily **DALLININAE** Beecher, 1893

Genus **RUGITELA** Muir-Wood, 1936

TYPE SPECIES. *Terebratula bullata* J. de C. Sowerby 1823.

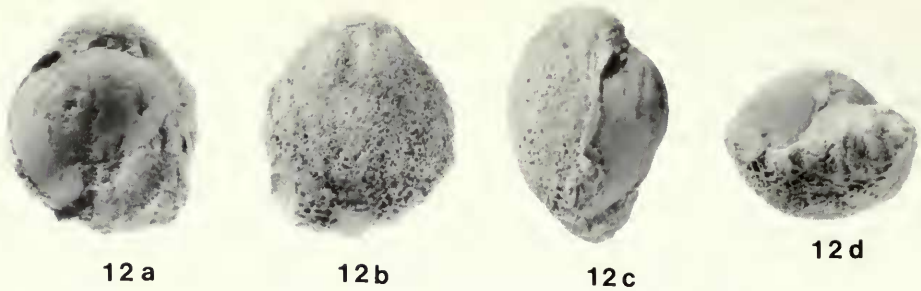


Fig. 12a-d *Rugitela? rotunda* sp. nov., Berriasian. **Holotype**, BB82395; Point Sublime, Alpes de Haute-Provence. $\times 3$.

Rugitela? rotunda sp. nov.

Figs 12, 13

HOLOTYPE. BB82395, from the Berriasian of Point Sublime, Alpes de Haute-Provence. Dimensions (mm), including adhering matrix: L 10.5, W 9.1, T 7.4.

PARATYPES. BB82396, which has been serially sectioned, and BB82397, both from the same locality and horizon as the holotype. MS/L 1583 and MS/L 1584 from the Upper Valanginian, north of Trigance, Var, Lyon University Collection. Dimensions (mm): BB82396 L 10.9+, W 9.6, T 8.8; BB82397 L 10.0, W 9.9+, T —; MS/L 1583 L 9.4, W 8.6, T 5.7; MS/L 1584 L 8.7, W 6.9, T 6.2.

NAME. 'Rotund', referring to the shape, especially of the brachial valve in lateral and anterior profile.

DIAGNOSIS. Rotund *Rugitela?* reaching the following approximate maximum dimensions: length 11 mm, width 10 mm, and thickness 9 mm. Circular outline. Incurved pedicle umbo, pedicle foramen small, circular and mesothyrid. Short, well-marked beak ridges. Lateral commissure straight, anterior commissure rectimarginate. V-shaped septalium, crural bases triangular.

DESCRIPTION. Shell smooth. The brachial valve has a circular outline and in lateral profile is nearly semicircular, flattened slightly in the anterior half. The pedicle valve, in lateral profile, has greatest convexity posteriorly, and is somewhat flattened in the middle third of its length. The pedicle umbo is incurved, often obscuring details of the pedicle foramen and the deltidial plates. A concave interarea is defined by subrounded beak ridges. No sulcus or carina is present in either valve.

Internal characters. The internal structures of one specimen have been investigated by serial sectioning (Fig. 13). The dental lamellae are weak and the pedicle collar has attached to it a

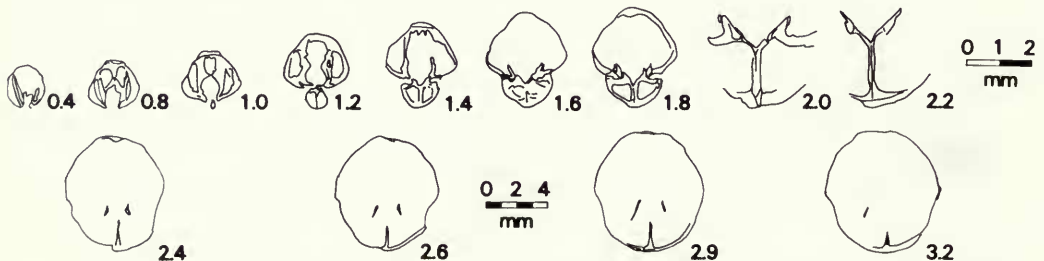


Fig. 13 Transverse serial sections through a paratype (BB82396) of *Rugitela? rotunda* sp. nov., Berriasian of Point Sublime, Alpes de Haute-Provence. Sections 2.0 mm and 2.2 mm are drawn at a larger scale. Dimensions (mm): L 10.9+, W 9.6, T 8.8.

small ventral septum (section 0.8 mm). A well-developed V-shaped septalium is supported by a median septum. The inner socket ridges are not deflected from the hinge plates. Anteriorly the median septum, hinge plates and crural bases form a Y-shaped outline (2.2 mm). The septalium is most acute in this section, and the wedge-shaped crural bases taper ventrally. The free crural bases are medially convex and the crural processes converge ventrally. The median septum was traced to section 4.2 mm.

REMARKS. Externally this species is very similar to the Jurassic brachiopods *Rugitela bullata* (J. de C. Sowerby) and the terebratulid genus *Sphaeroidothyris* Buckman. *R.?* *rotunda* can be distinguished from *Sphaeroidothyris* by its incurved pedicle umbo and the presence of a median septum and dental lamellae, often conspicuous by external examination. *R.?* *rotunda* is not known to have reached the dimensions of *R. bullata*. A sulcus is not developed in *R.?* *rotunda*, whilst in *R. bullata* it may give rise to ligate folding.

The evidence of internal structures only allows a provisional assignment to *Rugitela*. The thickening around the pedicle umbo and the presence of a small ventral septum is shared with other Lower Cretaceous genera, for example *Zittelina* Rollier. Muir-Wood's (1936: fig. 32) sections of *R. bullata* show thickening in the pedicle umbo. *R.?* *rotunda* has a wide and quite deep V-shaped septalium. The angle of the septalium is quite acute, comparable to that seen in *Zittelina wahlenbergi* (Zejszner) figured by Barczyk (1971: fig. 1). The typical W-shaped hinge plate configuration of *Rugitela* s.s. is not seen in *rotunda*, but both share medially convex, free crural bases which expand anteriorly and a persistent median septum. The lack of a median ridge in the septalium of *R.?* *rotunda* could be because of immaturity in the sectioned specimen. The septalium is similar to that seen in *Dzirulina*, but the wedge-shaped, ventrally pointing crural bases and their subsequent anterior development differ from that genus.

In *Advenina* gen. nov. (p. 188) the hinge plates are subhorizontal within the septalium. The acute septalium and more strongly developed dental lamellae of *R.?* *rotunda* help distinguish it from *A. oweni* sp. nov.

R.? *rotunda* can be distinguished from the similar-sized terebratulid *Hynniphoria globularis* Suess (1859) by its biconvexity of both valves, especially of the brachial valve, lack of the sulcate neanic shell seen in Suess' species and its characteristically well-marked shell endopunctuation. The dental lamellae in the pedicle valve of *H. globularis* are seen to diverge at about 90° when viewed ventrally, whilst in *R.?* *rotunda* they diverge at about 30°.

Dagys (1968) figured and sectioned a globose 'bubble-like' terebratulid from the Lower Volgian of Siberia, which he referred to *Russiella bullata* (Rouillier). The figured specimens are larger than any of *R.?* *rotunda* seen to date, and in profile lack the globosity of the brachial valve. In Dagys' material the brachial valve is somewhat flattened, whereas the pedicle valve is more convex than that of *R.?* *rotunda*. Internally it has a gently convex septalium from which the descending branches project anteriorly from the lateral edges.

The globose external morphology of *Rugitela?* *rotunda* is reminiscent of *R. bullata* (J. de C. Sowerby) of the Jurassic, but no direct link is inferred. Internally the features of *R.?* *rotunda* are comparable to *Rugitela*, but they are not typical.

HORIZON. Berriasian of Provence (bed 2, Fig. 3) and Upper Valanginian of Var.

MATERIALS AND LOCALITIES. Three specimens from Point Sublime, Alpes de Haute-Provence, BB82395-7. Four specimens from north of Trigrance, Var (Lyon University Collection), MS/L 1583-6.

Genus *ADVENINA* gen. nov.

TYPE SPECIES. *Advenina oweni* sp. nov.

NAME. From *advena*, 'newcomer'.

DIAGNOSIS. Oval, sub-pentagonal or sub-triangular in outline. Biconvex profile, smooth-shelled. Pedicle umbo erect, foramen of medium size, circular, mesothyrid. Deltidial plates disjunct or conjunct, may be obscured. Beak ridges sharp, defining broad interarea. Anterior commissure rectimarginate to uniplicate, crenulation may be developed. Lateral commissure straight.

Internal characters. Dental lamellae weakly developed. Septalium is well developed, acute posteriorly, anteriorly broadens and shallows, and is supported by a median septum. Septalium and median septum give Y-shaped outline in transverse section. Crural bases are given off at lateral edges of the septalium, closely associated with thickened inner socket ridges. Crural bases taper, giving a wedge shape in transverse section. Median septum persists anteriorly beyond the septalium and may extend to half total valve length or beyond. Crura stout, but rapidly extend into high crural processes. Remaining descending and ascending branches thin.

SPECIES INCLUDED. *Advenina oweni* sp. nov. Other specimens of *Advenina* have been described by Lobacheva (1966) under the names *Psilothyris tamarindus* (Sowerby), ?*P. (?) kouensis* (Moisseev) and *P. aff. faurei* (de Loriol).

RANGE OF GENUS. Berriasian?; Valanginian–Barremian.

REMARKS. *Advenina* is externally homoeomorphic with a number of Mesozoic terebratellids but can be distinguished by its internal structures. In *Advenina* the hinge plates are anteriorly sub-horizontal within the septalium. The acute septalium, more strongly developed dental lamellae and secondary callus thickening in the pedicle umbo of *Rugitela? rotunda* (p. 186) help to distinguish it from *A. oweni*.

The genus *Advenina* is proposed for brachiopods described from faunas of Tethyan and Jura affinities, associated with clay-rich sediments (in France and Switzerland), as are specimens of *Rugitela* (Owen 1973: 128). Lobacheva (1966) records specimens, referred herein to *Advenina*, from the Valanginian to Aptian of the Kopet Daga, although material of Hauterivian to Aptian age referable to *Advenina* has not been found in western Europe.

Internally *Advenina* lacks the median ridge which is often strongly developed in the septalium of *Rugitela*, and has not been seen to possess the secondary callus thickening in the pedicle umbo often present in the latter genus. The anterior commissure of *Rugitela* is sulcate or rectimarginate; in *Advenina* it is rectimarginate to uniplicate. In *Rugitela* the crural bases are given off dorsally, which, in conjunction with the median ridge, give rise to the W-shaped septalium, which is well developed in this genus. In *Advenina* the crural bases are given off at the lateral edges of the septalium producing a Y shape when the septalial plates, crural bases and median septum are still in contact, as seen in transverse section.

Advenina can be distinguished from the externally homoeomorphic genus *Dzirulina* Noutsoubidze 1945 by its internal structures. Externally both genera are circular in outline with an evenly biconvex profile, suberect pedicle umbo and circular mesothyrid (to permesothyrid) pedicle foramen. Incipient uniplication may be developed. Internally the two genera share weak dental lamellae, but the septalium is broader and flatter in *Dzirulina*. The acute Y shape of the ascending branches attached to the septal pillar in *Dzirulina* distinguishes it from *Advenina* where no attachment is seen.

Advenina oweni sp. nov.

Figs 14–18

1971 *Rugitella hippopus* (Roemer) (*sic*); Cotillon: 29.

1974 *Rugitela hippopus* (Roemer); Pajaud: 100, fig. D; pl. 2, fig. D.

1979 *Rugitela tamarindus* (Sowerby) (*sic*); Richter: 113; fig. 121.

HOLOTYPE. BB86852, from the Lower Valanginian of Carajuan, Alpes de Haute-Provence; from bed 5 of Fig. 3. The specimen measures (mm): L 14.5, W 12.5, T 8.6.

PARATYPES. BB86853–8 from the same locality and horizon as the holotype. BB86859 from the Lower Valanginian of Collet des Boules, south-east of Peyroules, Alpes de Haute-Provence. MS/L 1579 from the Valanginian of La Treille, Var; Lyon University Collection. Dimensions (mm): BB86853 L 13.4, W 11.7, T 8.2; BB86854 L 15.1, W 12.2, T 8.7; BB86855 (sectioned; Fig. 16) L 5.3, W 4.3, T 2.8; BB86856 L 9.9, W 8.6, T 6.2; BB86857 L 12.5, W 10.5, T 8.0; BB86858 (sectioned; Fig. 17) L 14.0, W 11.6, T 9.3; BB86859 (sectioned; Fig. 18) L 13.5, W 11.8, T 8.8; MS/L 1579 L 11.5, W 9.6, T 7.7.

NAME. After Dr E. F. Owen.

DIAGNOSIS. *Advenina* typically sub-triangular, from elongate-oval to sub-quadrate in outline. Maximum width in anterior half of shell. Anterior commissure narrowly uniplicate. Septalium U- to V-shaped. Persistent median septum, thickened crural bases given off ventrally.

DESCRIPTION. Pedicle umbo suberect, often broken to expose dental lamellae. Pedicle foramen of medium size, circular, mesothyrid, with beak ridges that border a quite wide concave inter-area. Deltoidal plates small, rarely visible. The anterior margin of the shell outline is straight-truncate to rounded, and may appear incipiently bilobate when the uniplication of the brachial valve has been slightly crushed. In the anterior third of the pedicle valve a narrow sulcus, about one-third of the valve's width or less, is developed. This is bordered by carinae. The sulcus may persist for two-thirds of the length of the pedicle valve from the anterior commissure. The pedicle sulcus is developed as a narrow, weak, dorsal uniplication of the anterior commissure, which may be 'pointed'. There is no distinct fold in the brachial valve anteriorly. Punctation is well marked and growth lines are faint, although in a few specimens they are well marked.

Internal characters. Serial sections of three specimens are presented here. Fig. 16 shows a series of serial sections taken from the smallest available for study, which measured (mm): L 5.3, W 4.3, T 2.8. The septalium is well developed at this early growth stage and is anteriorly supported by the median septum (1.4 mm). The crura are given off from the ventral edge of the hinge plates. The transverse band is dorsally concave. The median septum is long, increasing in height anteriorly (2.3 mm), and with the close proximity of the transverse band (2.5 mm) this suggests the campagiform phase had already been passed through, and that resorption of the hood had taken place.

An adult of *A. oweni* is represented by the series of sections in Fig. 17. The septalium widens anteriorly and the hinge plates become more horizontal too. The transverse band is not observed but the ascending branches are well preserved (6.8 mm).



Figs 14-15 *Advenina oweni* gen. et sp. nov., Lower Valanginian of Carajuan, Alpes de Haute-Provence. Fig. 14a-d, holotype, BB86852. $\times 3$. Fig. 15a-d, paratype, BB86853. $\times 3$.

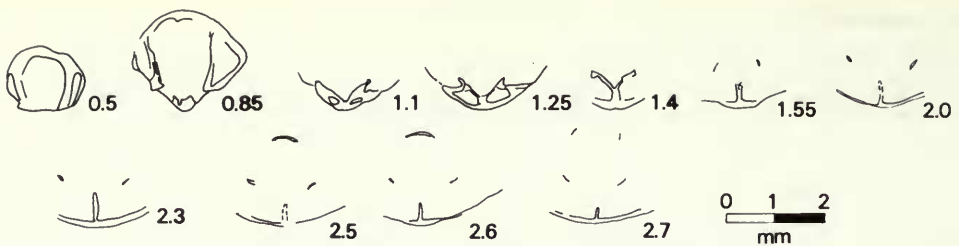


Fig. 16 Transverse serial sections through a juvenile paratype (BB86855) of *Advenina oweni* gen. et sp. nov.; Lower Valanginian of Carajuan, Alpes de Haute-Provence. Dimensions (mm): L 5.3, W 4.3, T 2.8.

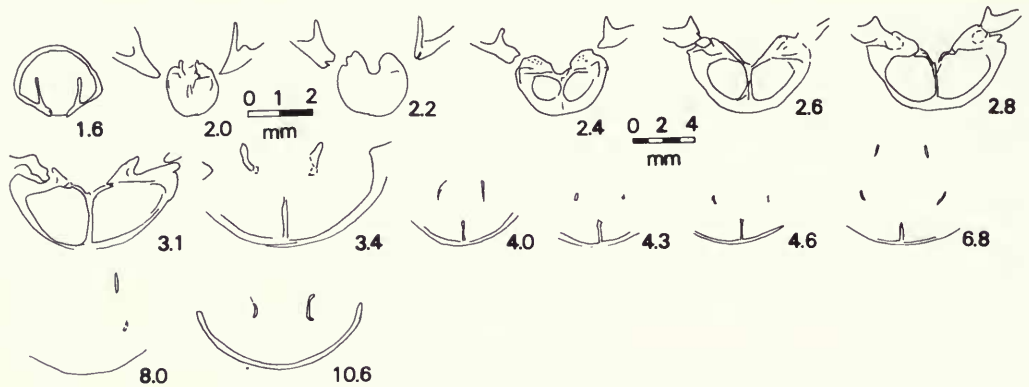


Fig. 17 Transverse serial sections through an adult paratype (BB86858) of *Advenina oweni* gen. et sp. nov.; Lower Valanginian of Carajuan, Alpes de Haute-Provence. Sections 2.0 mm to 3.4 mm are drawn at a larger scale. Dimensions (mm): L 14.0, W 11.6, T 9.3.

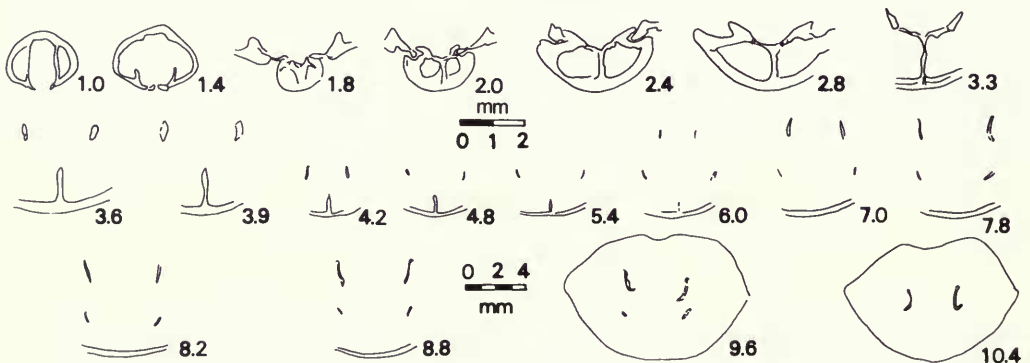


Fig. 18 Transverse serial sections through an adult paratype (BB86859) of *Advenina oweni* gen. et sp. nov.; Lower Valanginian of Collet des Boules, Alpes de Haute-Provence. Sections 1.8 mm to 3.9 mm are drawn at a larger scale. Dimensions (mm): L 13.5, W 11.8, T 8.8.

Fig. 18 shows a series of sections of an adult specimen of *A. oweni* from Collet des Boules. This shows the septalium very clearly, and the thickened shell in the vicinity of the inner socket ridge and socket floor. Anteriorly the crura develop near these thick inner socket ridges (3.3 mm) and the sub-horizontal hinge plates are well displayed. The descending branches curve laterodorsally and the ascending branches are sub-parallel.

No terminal or lateral spines have been observed on the descending branches on any of the

sectioned specimens. As these are fragile structures it is possible that they are not always preserved or they may be difficult to differentiate from the matrix.

REMARKS. Serial sections given by Lobacheva (1966: figs 23, 24) of specimens from the Hauterivian to Aptian of the Crimea, northern Caucasus, Georgia and Kopet Daga share a number of similarities with *A. oweni*. These specimens all share weak dental lamellae, and a broad, fairly shallow septalium lacking a median ridge, which is supported by a fairly persistent median septum. *A. aff. faurei* as figured by Lobacheva (1966: fig. 24) has an unusual development of the median septum, in that it splits into a dorsal and ventral component anteriorly and is then lost. This is seen as reflecting greater resorption of the septum in an adult (loop traced to 12.9 mm), but the septum is present again anteriorly, implying this is the site of former attachment of the hood. The crural processes are high (section 4.5 mm), comparable to those seen in *A. aff. oweni* (Fig. 20, section 4.1 mm), except that in *A. aff. faurei* the median septum has been resorbed.

A. oweni has a close resemblance externally to *Psilothyris tamarinda* (J. de C. Sowerby), but the former species has a more triangular outline (due to its more anterior maximum width) and also has a narrower sulcus in the pedicle valve. *A. oweni* differs from *P. occidentalis* Cooper by the more inflated profile of its brachial valve and its sub-triangular outline. Work in progress on *P. occidentalis* suggests that *Tamarella* Owen 1965 is a junior subjective synonym of *Psilothyris* Cooper 1955. *A. oweni* does not develop the elongation of the valves at the site of the uniplication seen in *?P. ullukolensis* (Moisseev) shown by Smirnova (1972). The latter species also has a wider and stronger uniplication, and a less inflated profile.

A. tamarindus, as shown by Lobacheva (1966), has a more circular outline than *A. oweni*. *Dzirulina faurei* (de Loriol) has its maximum width of outline more posteriorly placed than in *A. oweni*, and does not possess the uniplication typically developed in the latter species.

D. pseudojurensis (Leymerie) has a wider uniplication of the anterior commissure than that of *A. oweni*, and it lacks the bordering carinae. *A. oweni* has a convex pedicle valve and poorly exposed deltidial plates, and lacks the sub-pentagonal outline of *D. pseudojurensis*. *A. oweni* may rarely be cinctiform in outline, but this is usually owing to crushing of the anterior commissure, emphasizing the weak pedicle sulcus. There are, however, specimens of *A. oweni* which closely resemble *D. pseudojurensis* externally, and these have yet to be investigated internally.

D. regularis (Smirnova), from the Lower Hauterivian of the Crimea, appears more pentagonal in outline than *A. oweni* and has a rectimarginate anterior commissure. These comments also apply to the Lower Barremian *D. marianovkensis* (Moisseev) as shown by Smirnova (1972). *D. plana* (Smirnova) from the Barremian to Aptian of the northern Caucasus has a more cinctiform outline with more anterior maximum width, tends to have a less inflated brachial valve and lacks the uniplication of *A. oweni*. *D. haughtoni* Owen from the Upper Aptian of northern Zululand has a more circular outline than *A. oweni* and is incipiently uniplicate. The above species referred to *Psilothyris* and *Dzirulina* may also be distinguished from *A. oweni* by their internal structures. However, Smirnova (1972) only presented serial sections of one of the species now referred to *Dzirulina*, namely *D. plana* (Smirnova), the type species of her now invalid genus *Belothyris*.

Pajaud (1974: pl. 2, fig. D) figured a Lower Cretaceous brachiopod from Provence and referred it to *Rugitela hippopus* (Roemer). This specimen is now recognized as *Advenina oweni* sp. nov. The most striking difference externally is that *R. hippopus* is sulcate, whereas *A. oweni* is uniplicate.

HORIZON AND LOCALITIES. Lower Valanginian, Carajuan and Collet des Boules, south-east of Peyroules, Alpes de Haute-Provence (bed 5 of Fig. 3). Upper Valanginian of La Treille, Var. Berriasian? of Sarcenas, Isère, Grenoble University Collection. Pajaud (1974) records this species as *Rugitela hippopus* from the Upper Valanginian of La Martre-Châteauvieux, Var.

MATERIAL. Over two hundred specimens from Carajuan, including the holotype and six paratypes (BB86852-8). One hundred and thirty-seven specimens from Collet des Boules, including one paratype (BB86859). Two hundred and fifty-eight specimens from La Treille (Lyon University Collection), including one paratype (MS/L 1579).

Advenina aff. *oweni* sp. nov.

Figs 19, 20

REMARKS. In the collection of Neuchâtel University are five brachiopods referred to *A.* aff. *oweni*. The specimens are of Valanginian age, from Le Collaz, Ste Croix, Switzerland, from the Bourquin Collection. *A.* aff. *oweni* appears to be more variable than *A. oweni* from Provence. However, this may reflect the scarcity of specimens of *A.* aff. *oweni* from Le Collaz compared to the numerous specimens of *A. oweni* from Provence where morphologically intermediate forms link variants, showing the variability to be within one species. The Swiss specimens are subtriangular, with a similar lateral profile to the French material, and beak characteristics are comparable. One specimen (MS/N 1594) has an unusually highly inflated brachial valve posteriorly, but they all possess a uniplicate anterior commissure.

An interesting development of the anterior commissure is seen on the specimen of *A.* aff. *oweni* that has been serially sectioned (MS/N 1065). Small and very short crenulate folds are developed on the uniplication. This feature was also noted by de Loriol (1896) on '*Zeilleria favrei*', who commented on it as being a very variable feature. This crenulation is apparently rarely developed, although it would seem to be more common at Le Collaz among the few specimens as yet available.

The crenulation of the anterior commissure is an unusual feature among terebratelloids and its development must remain somewhat conjectural. It is known in *Dzirulina favrei* (de Loriol), and in ?*A. kouensis* (Moisseev) and *A.* aff. *favrei* both shown by Lobacheva, as well as in *A.* aff. *oweni*. Pictet & de Loriol (1872: 70) recorded some specimens of the terebratulid *Loriolithyris russillensis* (de Loriol) from the Valanginian limonite of Villers-le-Lac with multiple folds of the anterior commissure. This is comparable to the crenulation of the anterior commissure seen in the present form from the Valanginian of Le Collaz, but the crenulation is confined to the commissure in the latter species and not developed as discrete folds as in *L. russillensis* (Pictet & de Loriol 1872: pl. 202, fig. 6a-c). However, its development may be related to environmental conditions.

The matrix on and infilling the specimens of *A.* aff. *oweni* is a micritic limestone that has given a yellow-orange staining to parts of some specimens, showing it to be ferruginous, but more detailed information on the lithology from which they were collected is not available. Sedimentological information is also lacking for the forms described by de Loriol (1896) as '*Zeilleria favrei*', from the Lower Cretaceous of the Crimea, in which crenulation is developed on a rectimarginate to incipiently uniplicate anterior commissure. Crenulation in terebratellids is associated with maturity and is asymmetrically developed. If its formation were an adaptation for the exclusion of larger particles it might have developed earlier in growth, as this would be a constant requirement throughout life; in any case the crenulation is developed in what is generally accepted as the 'exhalent' part of the anterior commissure. The crenulation would have increased the surface area of the mantle epithelium, and this might have aided oxygen, or



Fig. 19a-d *Advenina* aff. *oweni* gen. et sp. nov., Valanginian. Plaster cast of sectioned specimen from Neuchâtel Collection, MS/N 1065; Le Collaz, Ste Croix, Switzerland. $\times 3$.

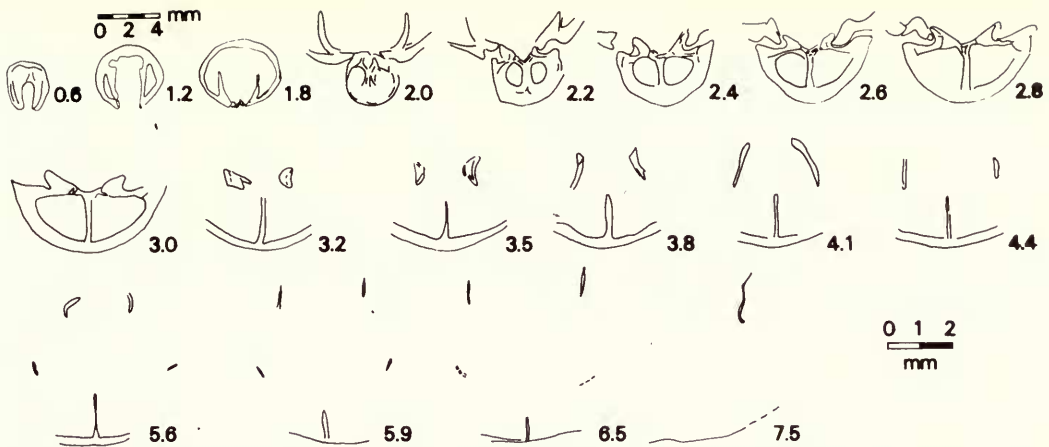


Fig. 20 Transverse serial sections through a specimen (Neuchâtel Collection, MS/N 1065) of *Advenina* aff. *oweni*; Valanginian of Le Collaz, Ste Croix, Switzerland. Sections 0.6 mm to 1.8 mm are drawn at a smaller scale. Dimensions (mm): L 12.5, W 11.1, T 8.0.

nutrient, assimilation. Crenulate *Loriolithyris russillensis* and *Advenina* aff. *oweni* both appear to be associated with iron-bearing sediments.

Internal characters. One specimen of *A.* aff. *oweni* was serially sectioned to determine its relationship to the Provençal material. Internally the specimen has weakly developed dental lamellae and an initially acute septalium which becomes wider and shallower anteriorly. The inner socket ridges and hinge plates form a wedge-shaped outline, tapering towards the median septum (Fig. 20, section 2.8 mm). The crura are more strongly medially convex than those seen in the French specimens of *A. oweni*. The crural processes are quite high (4.1 mm). The configuration of the descending branches is similar to that seen in *A. oweni* (Fig. 18). The median septum is persistent and is slightly swollen on its ventral edge in sections 4.1 and 4.4 mm, possibly indicating a site of former hood attachment, comparable to section 4.0 mm of Fig. 17.

HORIZON AND LOCALITY. *Advenina* aff. *oweni* is recorded from the Valanginian of Le Collaz, Ste Croix, Switzerland.

MATERIAL. Five specimens from Le Collaz; Bourquin Collection, Neuchâtel University. Specimen numbers MS/N 1065 (sectioned; Fig. 20), MS/N 1592–5.

Conclusions

In Europe the migration of brachiopods from platform areas, for example the Jura, to continental margins (sub-Tethyan, that is, between Jura Platform and deeper water Tethyan facies) is believed to be the response of these benthonic organisms to the end-Jurassic regression, leading to a polarization of Tethyan and Boreal brachiopod faunas during the Tithonian and Berriasian. *Rhynchonella*, *Rugitela* and *Ornithella* are associated with clay-rich sediments and have a Boreal distribution, whilst *Lacunosella* and *Zittelina* occur in micrites and *Juralina* and *Weberithyris* in peri-reefal and reefal limestones of the Tethyan realm. *R. cotilloni* is a Lower Cretaceous exception for the genus by occurring in Tethyan micritic limestones. *Ornithella farquharsoni* (Muir-Wood, 1935) from the Lower to Middle Kimmeridgian of Somalia shows this genus to be widespread, and the Lower Cretaceous genus *Advenina* described from Tethys and the Jura may be derived from the dominantly Boreal genus *Rugitela*.

Thomson & Owen (1979: 35) stated 'It is clear that several "Northern Hemisphere" genera are more widely distributed than previously appreciated . . .' and the occurrence of *Rhynchonella cotilloni* in Provence would tend to confirm this. *Rhynchonella proeminens* Yin is tentatively referred to *R. s.s.*, this Tithonian species thus providing a link with the Boreal Portlandian

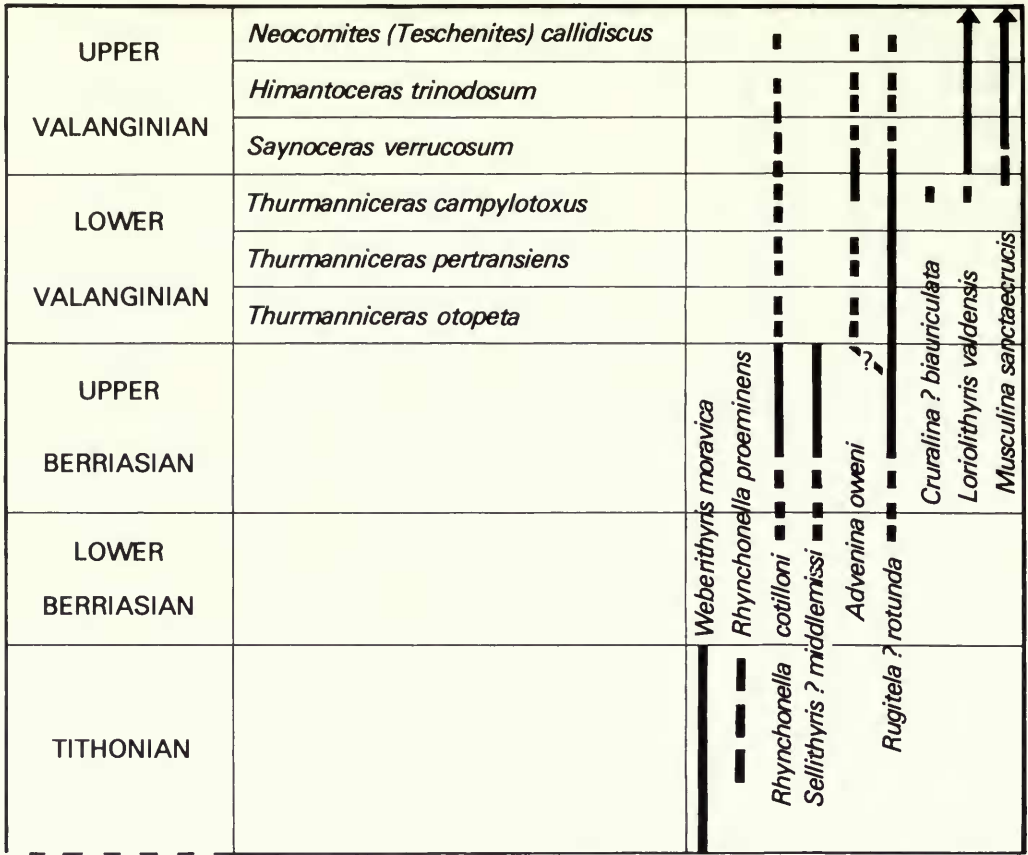


Fig. 21 Stratigraphical ranges of brachiopods from Provence and beyond, referred to in this paper.

species and those of the Lower Cretaceous of Provence. This supports Ager, Childs & Pearson's suggestion (1972: 224) that in post-Kimmeridgian times *R. s.s.* diversified into shallower-water habitats.

Sellithyrus is first represented in the Berriasian by *S. carteroniana* (d'Orbigny) in the southern French Jura (p. 179). *S.?* *middlemissi* sp. nov. is at present known only from the Berriasian of Provence. The association of species of *Rugitela* with clay-bearing sediments has already been noted (Owen 1973: 128). *Rugitela?* *rotunda* sp. nov. from the Berriasian is associated with micritic limestones in Provence. This small species may represent a sub-Tethyan diversification of the genus and possibly a paedogenetic offshoot from *Rugitela s.s. R.?* *rotunda* possesses secondary callus thickening in the pedicle umbo, a feature which has not been observed in *Advenina oweni* sp. nov. The former species also has more strongly developed dental lamellae and a more acute septalium. The two species differ by external and internal details but *R.?* *rotunda* does not appear to be far removed from *Advenina* gen. nov., both lacking a median ridge in the septalium.

Sellithyrus? *middlemissi*, *Rhynchonella cotilloni* and *Rugitela?* *rotunda* are stratigraphically distinctive, occurring in the Berriasian, the latter two species ranging into the Upper Valanginian (Fig. 21), whilst *Advenina oweni* is recorded from the late Lower Valanginian of Provence and ranges into the Upper Valanginian.

The brachiopod fauna described from the Berriasian–Lower Valanginian of Provence suggests that a number of new species are associated with the Lower Cretaceous marine transgressions, and may indicate a 'speciation event'.

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